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LARVAL DEVELOPMENT OF THE NORTHERN HORSE MUSSEL, *MODIOLUS MODIOLUS* (L.), INCLUDING A COMPARISON WITH THE LARVAE OF *MYTILUS EDULIS* L. AS AN AID IN PLANKTONIC IDENTIFICATION[1]

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The northern horse mussel, *Modiolus modiolus* (L.), is found along the coasts of North America from the Arctic Seas to New Jersey, and from the Bering Sea to San Pedro, California (Abbott, 1974). Its global range includes the coasts of Japan, Iceland, Europe, northwestern Africa, and the Mediterranean countries (Madsen, 1949; Rowell, 1967). It is primarily a subtidal species, inhabiting rocky and gravelly bottoms to a depth of 280 meters (Wiborg, 1946; Madsen, 1949; Rowell, 1967).

The spawning season of *M. modiolus* is ill-defined and may vary greatly with depth and geographical location. It has been suggested that major spawnings occur at intervals of several years, with the possibility of partial spawnings one or more times each year (Wiborg, 1946; Rowell, 1967). Release of gametes has been observed from February through July in European waters (Nordgaard, 1901; Williamson, 1907; Wiborg, 1946).

Early efforts to establish the identity of *M. modiolus* larvae in the plankton were inconclusive, and as Jørgensen (1946, p. 289) states, "the resemblance to the *Mytilus edulis* veliger may be so great that a confusion of these two species may have taken place." Although Rees (1950) and Newell and Newell (1963) compared the larval forms of these two closely related mytilids, their identification of *M. modiolus* relied on the error-prone "indirect method" (see discussion in Loosanoff, Davis, and Chanley, 1966), and subtle differences in shape, color, and texture constituted the only distinguishing features between the two veligers.

Laboratory work with larval *M. modiolus* has been nearly nonexistent. Nordgaard (1901) carried larvae through the straight-hinge stage, but inadequate culture techniques prevented the observation of further development. Williamson (1907) witnessed a natural spawning of adult horse mussels in the laboratory but made no attempt to rear larvae. The present study provides a detailed description of laboratory-cultured *M. modiolus* larvae from the straight-hinge stage to metamorphosis, including photographic and statistical comparisons with *Mytilus edulis* L. to aid in differentiating the two species.

Materials and Methods

Sexually mature adult horse mussels were collected subtidally along the coast of Chamberlain, Maine, and were placed in a running saltwater bath at approximately 14° C. Attempts to spawn the mussels by transferring them to a warm (20° C) water bath, by rapidly fluctuating the water temperature, and by adding

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stripped gametes to the water were generally unsuccessful. The few fertilized eggs thus obtained showed slow and abnormal development. Thermal stimulation followed by individual injections of 0.5 M KCl, as described by Bayne (1965), also proved ineffective in inducing release of gametes. On one occasion, however, spawning occurred spontaneously when the water flow through the holding tank was temporarily stopped.

Eggs from this spontaneous spawning were transferred to a 55 l polyethylene tank, which was filled with sea water filtered to remove particles 1 μ or larger in diameter. Numerous eggs were also pipetted along with culture water onto a glass slide (no coverslip) and photographs taken for subsequent measurements of fertilized egg diameters. After 72 hrs larvae were transferred to a 16 l polyethylene container and adjusted to a low density (1–5/ml) to minimize growth rate reductions due to crowding. The temperature of the culture ranged between 16° and 21.5° C, and salinity varied little from 30‰. Filtered sea water was used to change the cultures every other day, at which times larvae were collected for preservation in 95% EtOH. Larvae were fed daily with concentrations of *Isochrysis galbana* Parke ranging between 30,000 and 80,000 cells per ml of culture. Techniques for handling eggs and larvae followed closely those described by Loosanoff and Davis (1963).

Several adult specimens of *M. edulis* were conditioned and spawned according to the procedure outlined by Bayne (1965), and cultures of these larvae were also carried through metamorphosis using the techniques of Loosanoff and Davis (1963). Larvae were sampled every other day and preserved in 95% EtOH.

The micrographs and length-height measurements for this study were obtained from whole larvae, taking care to achieve consistent and representative larval orientations. Obtaining such consistent orientations, however, is rendered difficult by the convex shape of intact specimens. Nevertheless, dissociating the two valves is a tedious process and most routine plankton identifications will utilize only the intact bivalve. Loosanoff, Davis, and Chanley (1966) have discussed problems associated with the identification of bivalve larvae, including the relative merits of using whole larvae or single valves in photomicrograph sequences and the worth of various dimensional measurements.

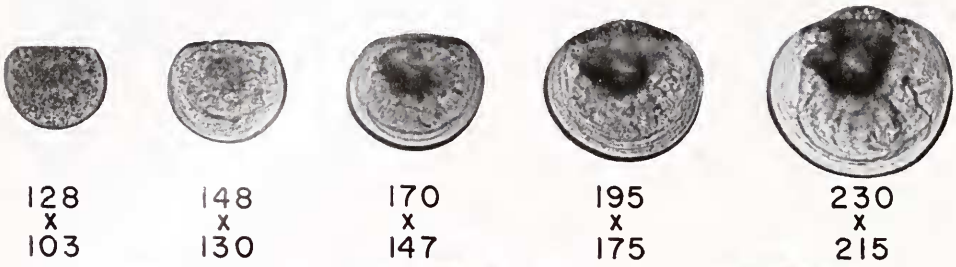
Preserved larvae of both species were measured to the nearest 5 μ with a calibrated ocular micrometer, and values for hinge-line length, total length, height, and depth were obtained. Three-dimensional growth diagrams were constructed using the method described by Chanley and Van Engel (1969). A Cambridge S-4 scanning electron microscope was used to examine the surface shell morphology of individuals from the straight-hinge stage through metamorphosis. Descriptive terms are defined in Chanley and Andrews (1971).

Results

Larval development of Modiolus modiolus

Fertilized eggs measured from 78 to 90 μ in diameter with a mean of 85 μ. Development through the ciliated gastrula and trochophore stages was similar to that described by Field (1922) for *M. edulis*. The elongate, somewhat conical trochophore displayed a prominent apical flagellum on its larger end.

Modiolus modiolus



128 x 103 | 148 x 130 | 170 x 147 | 195 x 175 | 230 x 215

260 x 245 | 310 x 290 | 340 x 315

Mytilus edulis

100 x 70 | 130 x 103 | 148 x 118 | 165 x 140 | 190 x 163

225 x 200 | 265 x 240 | 285 x 265

The smallest shelled veliger observed had length, height, and straight-hinge dimensions of 105, 90, and 95 μ, respectively. The distribution of hinge-line lengths remained constant over time, with a mean of 100 μ and extremes of 90 and 110 μ. As total lengths reached 150 to 165 μ the hinge-line was obscured by the appearance of a low, rounded umbo, which subsequently developed into a knobby protrusion (Figs. 1, 2). As with most mytilids (Chanley, 1970), the anterior end of umbo stage individuals was more pointed than the posterior end.

Measurements of 745 larvae from early straight-hinge through the pediveliger stage were used to run a linear regression of height on length, giving the relationship: height = 1.04 length − 29.26 ($r^2 = 0.98$). The same calculation for 89 length *versus* depth observations yielded the equation: depth = 0.67 length − 16.90 ($r^2 = 0.97$). In Figure 3 these length-height and length-depth data are combined to give an approximate three-dimensional representation of minimum and maximum sizes over the entire larval period.

The apical flagellum was still visible on the velum of the shelled larvae up to total lengths of 260 μ (Fig. 5B); whether or not it was present beyond that point was not ascertained. As larvae attained lengths of 230 to 245 μ, the nascent larval foot was evident posteriorly within the shell. Pigmented eyespots began appearing as larvae exceeded 270 μ in size, and the full-grown foot of the pediveliger stage became functional as larvae surpassed 295 μ in length. Eyespots measured 6 to 10 μ in diameter.

Scanning electron micrographs of the exterior hinge region (Fig. 2) reveal no distinctive features such as taxodont teeth or asymmetry of the left and right valves. Lack of growth in hinge length, however, indicated previously by near-constant straight-hinge measurements, is further evidenced by the clear delimitation of the hinge structure at either end of Prodissoconch I. Similar micrographs of the surface of the left valve (Fig. 2) demonstrate the sharp boundary between Prodissoconchs I and II as well as the concentric ridges of Prodissoconch II.

Although the culture was not maintained at a strictly constant temperature, times for the development of certain larval features in *M. modiolus* at culture temperatures of 16–21° C can serve as a general basis for comparison with other bivalve larvae. Day of fertilization equals day zero. Approximate time to the first straight-hinge larvae is 40 hrs; rounded umbo, 8 days; knobby umbo, 13 days; developing foot visible inside shell, 13 days; eyespot, 17 days; active foot, 18 days; first settled larvae, 19 days.

On any given day the culture contained a wide range of larval sizes, and the extent of the size range increased with time. At 2 days shell lengths were evenly distributed between 105 and 140 μ, a spread of 35 μ. At 11 days lengths varied over a range of 60 μ, and by 17 days larvae differed in length by as much as 100 μ.

Larval development of Mytilus edulis

The diameter of fertilized eggs averaged 67 μ. Observations on cleavage and embryological development up to the shelled veliger stage agreed closely with the

FIGURE 1. Photomicrographs of the larvae of *Modiolus modiolus* and *Mytilus edulis* from the early straight-hinge stage to metamorphosis. Length and height dimensions are given in microns below the individual specimens. Larvae are oriented with the anterior end to the left.

comprehensive description given by Field (1922). The trochophore possessed a distinct apical flagellum which persisted throughout subsequent larval development.

Measurements of newly-shelled straight-hinge larvae gave minimum length, height, and hinge-line dimensions of approximately 95, 70, and 70 μ, respectively.

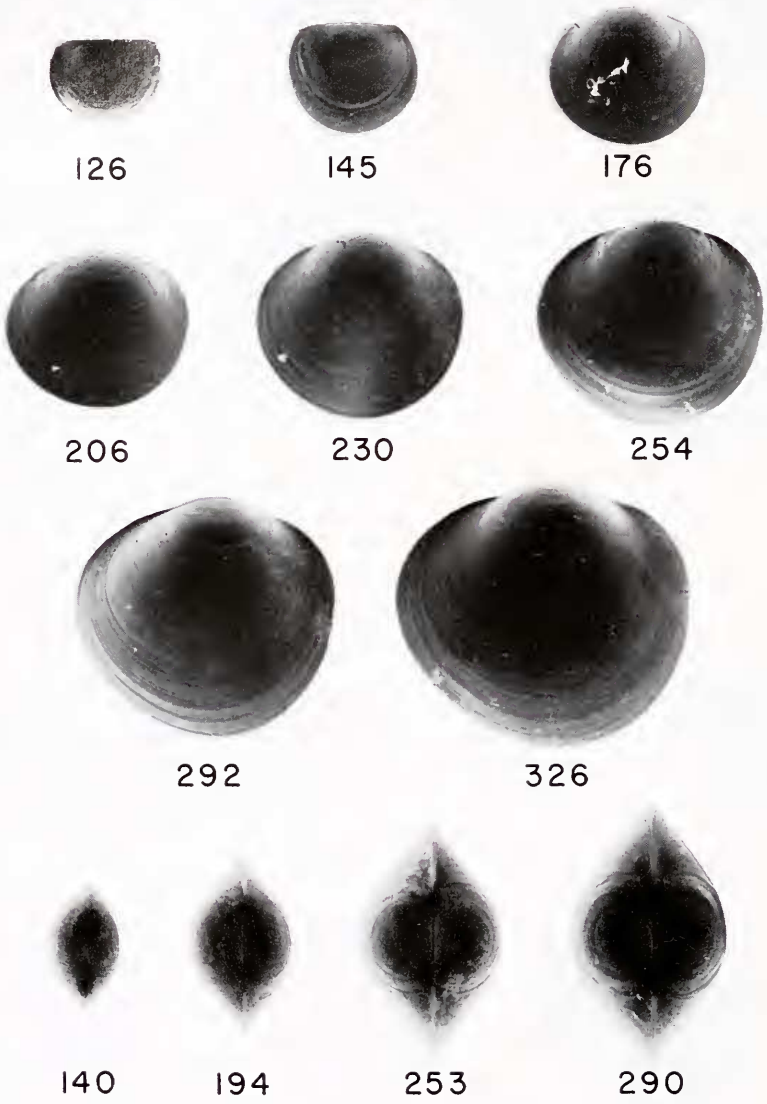


FIGURE 2. Scanning electron micrographs of the larvae of *Modiolus modiolus* from early straight-hinge stage to metamorphosis. Photographs in the top three rows depict the shell surface morphology of the left valve, while those in the bottom row represent a dorsal view of the hinge region. Length dimensions are given in microns below each specimen.

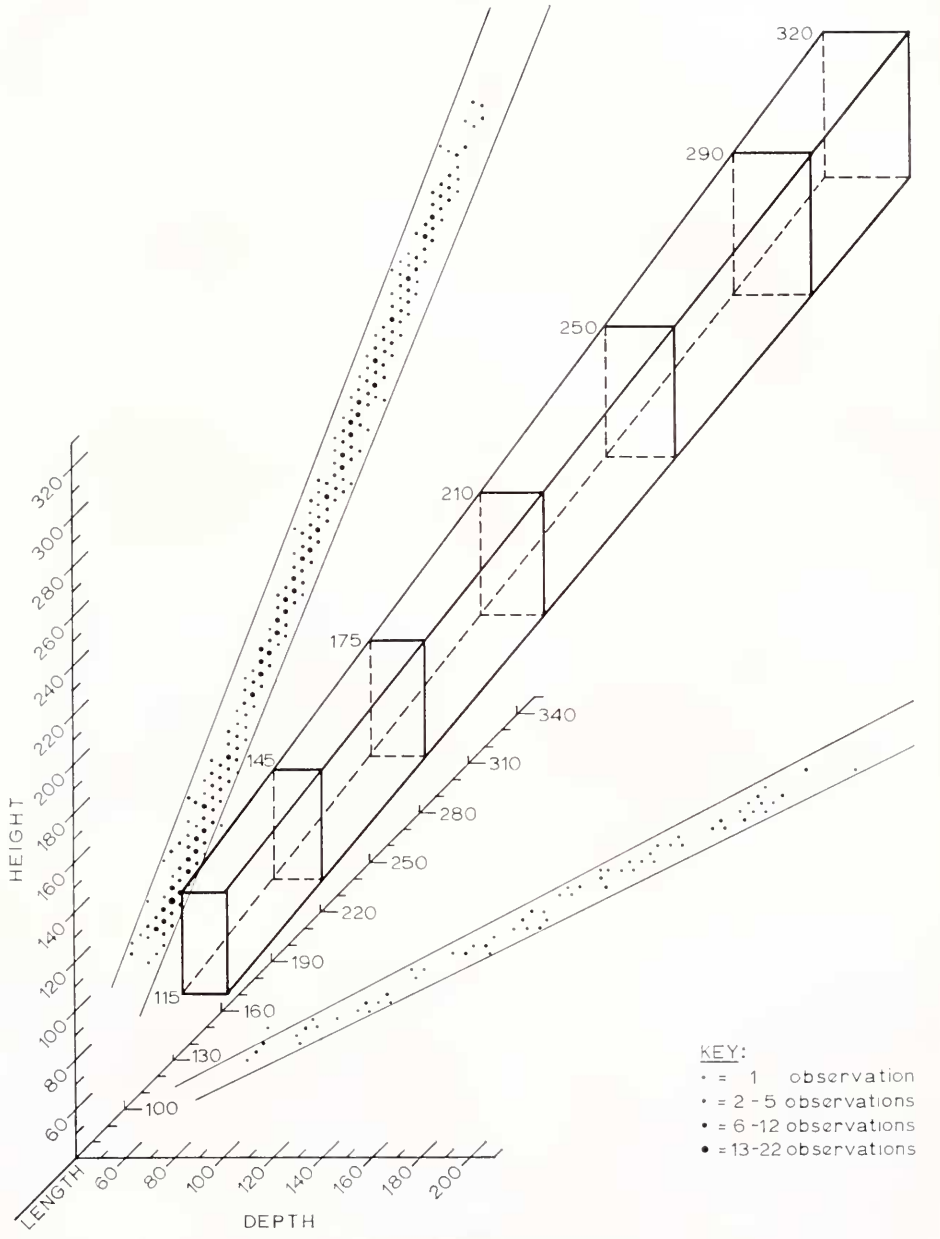


FIGURE 3. Larval dimensions of *Modiolus modiolus*. Height and depth coordinates run parallel to the length axis. Dots represent observed length-height or length-depth measurements. The polyhedron was constructed according to the procedure outlined by Chanley and Van Engel (1969) and encompasses all possible length-depth-height combinations of *M. modiolus* larvae.

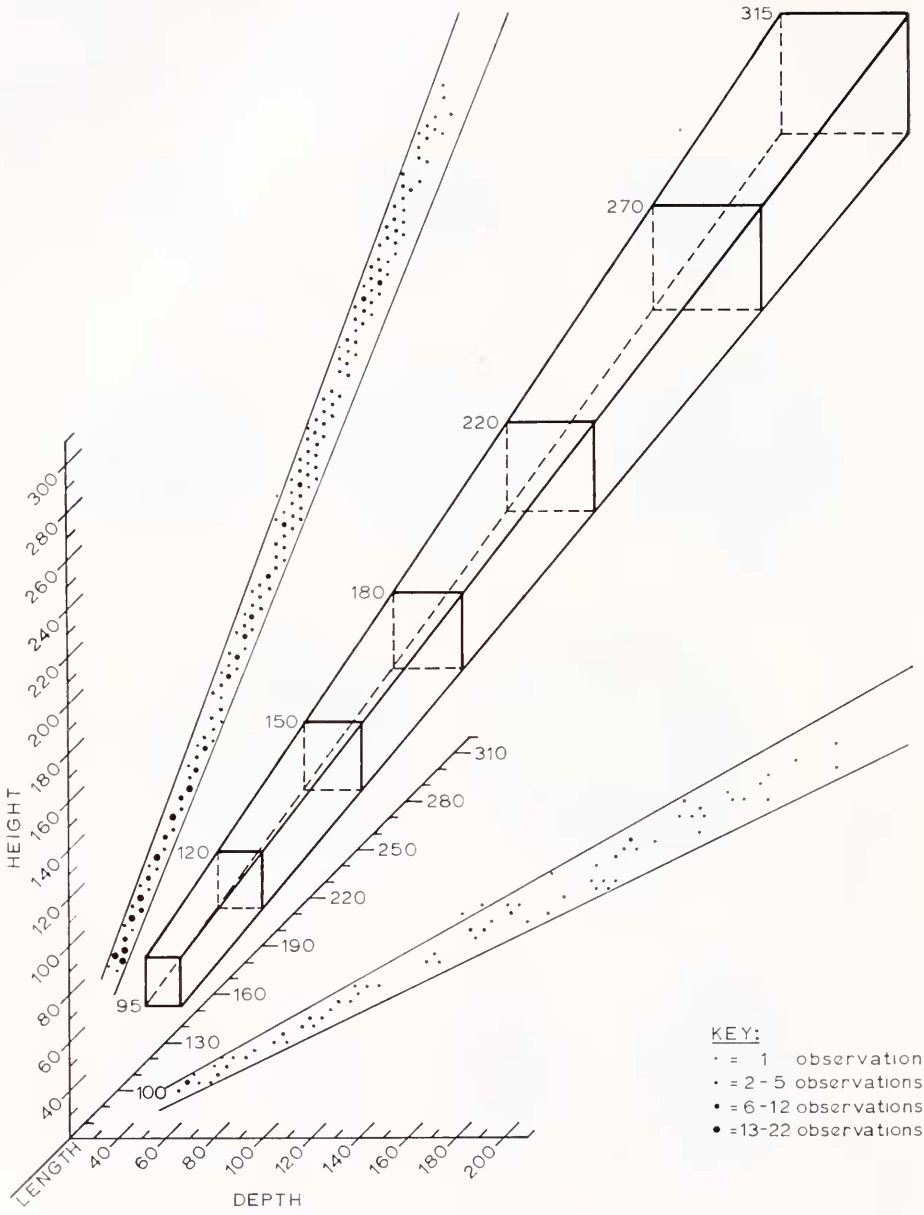


FIGURE 4. Larval dimensions of *Mytilus edulis*. Height and depth coordinates run parallel to the length axis. Dots represent observed length-height or length-depth measurements. The polyhedron was constructed according to the procedure outlined by Chanley and Van Engel (1969) and encompasses all possible length-depth-height combinations of *M. edulis* larvae.

Hinge-line lengths ranged from 70 to 80 μ, with the mean remaining constant over time. When larvae reached 140 to 150 μ in total length, the appearance of a rounded umbo marked the transition from the straight-hinge to the umbo stage of development. As larvae grew past 210 to 230 μ in length, the umbo gradually extended from the hinge and shoulders as a low knob (Fig. 1).

A linear regression of height on length, run on data from 550 *M. edulis* veligers in all stages of development, yielded the equation: height = 1.08 length − 37.22 ($r^2 = 0.99$). Eighty-eight length *versus* depth measurements were used in a similar fashion to calculate the equation: depth = 0.61 length − 15.82 ($r^2 = 0.96$). The length-height and length-depth data were then combined to create a three-dimensional approximation of maximum and minimum larval sizes for the entire shelled veliger stage (Fig. 4).

Eyespots were detected in larvae as small as 205 μ long, although the majority developed them when shell lengths reached 220 to 230 μ. Larvae as large at 245 μ were occasionally observed to lack an eyespot. The eyespot diameter varied from 5 to 7 μ. A well-defined foot could be seen in larvae 195 to 210 μ in length, and active extension of this organ began in larvae between the lengths of 215 and 240 μ.

As with *M. modiolus*, scanning electron micrographs of the exterior hinge

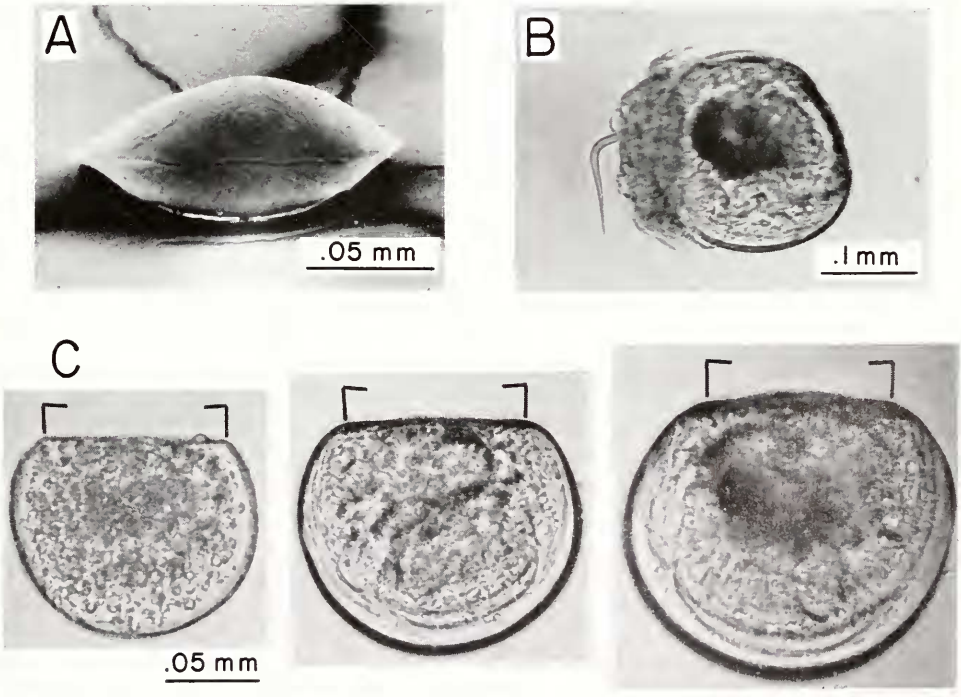


FIGURE 5. (A) Scanning electron micrograph of the hinge region of a straight-hinge veliger larva of *Mytilus edulis;* (B) early umbo stage larva (*Modiolus modiolus*) showing prominent apical flagellum; (C) various stages of development of straight-hinge larvae of *Modiolus modiolus.* Brackets delimit the "hinge-line" as measured in this study.

region revealed no asymmetry of the left and right valves, nor did they show any external manifestation of hinge teeth (Fig. 5A).

Discussion

Obtaining viable sperm and eggs appears to be the greatest barrier to more extensive work with *M. modiolus* larvae in the laboratory. The natural spawning which was observed upon cessation of the water current in the holding tank is identical to an experience reported by Williamson (1907) in his work with *M. edulis*. Subsequent attempts to reproduce this phenomenon and to thus establish a reliable means of spawning the horse mussel proved ineffective. Since thermal, chemical, and sex product stimulation of sexually mature individuals also failed to induce spawning in this species, exploration of other methods would be highly desirable. Electrical stimulation (Iwata, 1950; Sugiura, 1962) and pricking of the posterior adductor muscle (Loosanoff and Davis, 1963) have successfully induced release of gametes in *M. edulis,* while artificial fertilization of stripped eggs and sperm has resulted in healthy larvae in some species (Loosanoff and Davis, 1963). Should these methods prove ineffective in themselves, long-term thermal conditioning may render the adults more susceptible to such stimuli.

The fertilized egg diameter range (78–90 μ) for *M. modiolus* observed in this study, is compatible with Williamson's (1907) reported value of 0.1 mm, as his value was only given to the nearest tenth of a millimeter. Wiborg (1946), however, gave a range of 0.09 to 0.14 mm, with an average of 0.10 to 0.11 mm. These measurements differ considerably from the observations made in this study. As Wiborg (1946) failed to state the conditions under which the egg diameters were measured, it is only possible to speculate on factors responsible for the observed differences. The presence or absence of a coverslip or osmotic swelling or shrinkage due to different salinities during measurement might account for the discrepancies. It is also possible that the different reported diameters may be a morphological manifestation of subspecific variation between mussels from geographically isolated populations. A much more detailed study would be required to ascertain the existence of such subspecific differences.

The wide range of sizes for larvae of the same age and living in the same environment is a phenomenon common to many bivalve molluscs, as noted by Loosanoff and Davis (1963), and is most likely due to normal genetic variation. The point at which *M. modiolus* larvae reached a certain stage of development, however, seemed to be more dependent on size than on age. For example, the first larvae to possess an eyespot or an active foot were also the largest larvae in the culture on that day, the proportion of individuals possessing such characteristic features generally equaling the proportion of these larger individuals in the total population. Even when a sizable spatfall was visible on the container bottom, smaller individuals in the culture had not yet reached the pediveliger stage. Loosanoff and Davis (1963) and Loosanoff, Davis, and Chanley (1966) discussed evidence which shows that size at metamorphosis is independent of the geographical origin of the parents for several species of bivalve larvae, and independent of culture temperature for at least one species (*Mercenaria mercenaria* (L.)). Similarly,

Bayne (1965), in his work with *M. edulis*, noted that individual larvae seldom reached the pediveliger stage before 250 μ. Although individuals show small variations in the size at which a characteristic feature appears, results such as these demonstrate the validity of correlating larval dimensions with stages of larval development for identification purposes.

Many authors have presented descriptions of the development and settling behavior of *M. edulis* (Stafford, 1912; Field, 1922; Werner, 1939; Sullivan, 1948; Bayne, 1964, 1965; Chanley and Andrews, 1971). Only data pertinent to a quantitative comparison with *M. modiolus* larvae were gathered for the present study. Williamson (1907) and Field (1922) gave values for the diameter of *M. edulis* eggs (0.06 to 0.07 mm and 0.07 mm, respectively) which agree well with the average value of 67 μ in this study. The minimum dimensions for straight-hinge veligers offered by Sullivan (1948) (length $\times$ width values of 155 $\times$ 120 μ) are much larger than those observed in this study but the smaller veligers could have been absent from her plankton tow samples. Data from the laboratory cultures of Chanley and Andrews (1971) are in close agreement with the data of this study, yielding minimum length, height, and depth measurements about 5 μ smaller and nearly identical observations on the lengths at which the umbo, eyespot, and pediveliger foot develop.

The results in this study suggest that *M. edulis* and *M. modiolus* straight-hinge veligers are readily distinguished by the difference in their hinge-line lengths. Both species maintained a constant distribution of hinge-line lengths over time, with the *M. edulis* hinge averaging 74 μ long and that of *M. modiolus* averaging 100 μ long. The largest hinge measurement for *M. edulis* was 80 μ and the smallest for *M. modiolus* was 90 μ, making this a definite means of differentiating between younger larvae of the two species. This conclusion, however, should be viewed with a certain degree of caution. Hinge-line lengths of *M. edulis* larvae recorded in this study are restricted to a somewhat narrower range than the 65–85 μ range reported by Chanley and Andrews (1971). In addition, Chanley (1970) and Chanley and Andrews (1971) reported a slight increase in the length of the hinge-line of most mytilids (including *M. edulis*) with larval growth. Such an increase was not observed for either of the species examined in the present study. The differences between their results and those of the present study can be accounted for by their inclusion of the straight dorsal extremities of the larval shoulders in their "straight-hinge" measurements of larger larvae (Chanley, personal communication). Actually the hinge-line is a Prodissoconch I character and, as with other bivalves, does not change with larval growth. In order to adequately distinguish this hinge-line from the dorsal extremity of each shoulder of relatively large *M. edulis* and *M. modiolus* larvae, it is necessary to focus up and down with the microscope until the hinge itself is in the plane of focus. Under such viewing conditions, the outside boundaries of the hinge-line generally coincide with the points at which the relatively flat dorsal region of the shell begins to gradually slope ventrally. It is recommended for future consistency that the "hinge-line" be considered as the dorsal region of the shell between these points. Representative photographs of several straight-hinge stages (*M. modiolus* in this case) are marked in Figure 5C in an attempt to delimit the "hinge-line" as defined in this manner. Determining the

points at which the shell begins to slope ventrally (even though the change in slope may be very slight) is felt to be much less subjective than attempting to pinpoint the outside boundaries of the hinge-line at specific places along the constantly sloping shoulders of the dorsal region. Werner (1939), in his work with North Sea plankton samples, reported an average hinge-line length for *M. edulis* of 93 μ. While such a measurement may reflect a morphological (perhaps subspecific) variation between North Sea *M. edulis* populations and those of the western North Atlantic, it is probably more reasonable to conclude that some of Werner's larval identifications, being based upon the "indirect method," were in error.

Distinguishing small *M. edulis* and *M. modiolus* straight-hinge veligers from one another is also possible through a comparison of total shell lengths. The smallest *M. modiolus* larvae observed measured 105 μ long by 90 μ wide, a clear 10 μ longer than the smallest *M. edulis* veliger. A simple length measurement in the 95 to 105 μ range can eliminate confusion between these two mytilids.

A comparison of the *M. edulis* and *M. modiolus* length-height scatter diagrams (Figs. 3, 4) shows them to be very similar. The length-depth measurements (Figs. 3, 4), however, demonstrate the fact that *M. modiolus* larvae (regression equation: depth = 0.67 length − 16.90) are generally of greater depth than *M. edulis* larvae (regression equation: depth = 0.61 length − 15.82). This fact should be used with caution in larval identification, since the larger *M. edulis* depth measurements at a given length often extend into the range of the corresponding *M. modiolus* depth sizes.

Careful examination of shell shape is also helpful in discriminating the larval forms of these two closely related Mytilidae. As noted by Newell and Newell (1963), the umbo of *M. modiolus* is generally more prominent than that of *M. edulis* for larvae of comparable sizes. In addition, at lengths greater than 200 μ, larvae of *M. modiolus* present a much more rounded appearance than those of *M. edulis*, with the anterior end of the latter being considerably more pointed than that of the former. This observation is diametrically opposite of that reported by Rees (1950) and casts doubt upon the accuracy of his indirect larval identifications of the two mytilids.

In the present study the larval stages of *M. modiolus* were found to be more opaque than those of *M. edulis*. As the shell of *M. modiolus* is generally of greater depth than that of *M. edulis*, it is suggested that the more opaque appearance of *M. modiolus* may be a reflection of relatively greater thickness of soft body parts.

As evidenced by examination of the scanning electron micrographs presented in this study, examination of the external hinge structure is of little or no value in distinguishing the two species. While such a discrimination may well be possible through careful examination of the internal hinge structure, the removal of individual valves is tedious and usually impractical for routine identifications in plankton samples (Chanley and Andrews, 1971).

In plankton samples containing live or well-preserved larvae, the presence of an eyespot in individuals with lengths less than 270 μ may be helpful in distinguishing *M. edulis* larvae from those of *M. modiolus*. In *M. edulis*, eyespots were observed in larvae as small as 205 μ, while such structures were not seen in *M. modiolus* until the larvae had attained a size of 270 μ.

The presence of a well-developed larval foot should also aid in discriminating the two species. In *M. modiolus*, the full grown foot of the pediveliger stage does not appear to become active until the larvae attain a length of at least 295 μ. In contrast, the larval foot of *M. edulis* was observed to be functional in larvae with lengths as small as 215 μ.

In the present study larvae of *M. modiolus* were found to attain a much greater length than those of *M. edulis* prior to settlement and metamorphosis. Maximum shell length of the larvae, however, is probably of little aid in distinguishing the two mussels in the plankton. Bayne (1965), while studying the delay of metamorphosis of *M. edulis* larvae, found a significant correlation between mean maximum size and temperature, encountering larval *M. edulis* with lengths up to 415 μ. It is reasonable to assume that *M. modiolus* may also be capable of achieving such lengths (perhaps even greater) under various environmental conditions.

While the present study has stressed a comparison between *M. modiolus* and *M. edulis*, the data presented should be of assistance in distinguishing these species from other mytilids. A comprehensive summary of larval characteristics of the Mytilidae is presented by Chanley (1970).

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Summary

1. Spontaneous spawning of *Modiolus modiolus* occurred under laboratory conditions at a temperature of approximately 14° C, and larvae were successfully cultured through settlement and metamorphosis.

2. Fertilized egg diameters varied from 78 to 90 μ with a mean of 85 μ.

3. The smallest shelled veliger observed had length, height, and straight-hinge dimensions of 105, 90, and 95 μ, respectively. The distribution of hinge-line lengths remained constant over time, with a mean at 100 μ and extremes of 90 and 110 μ.

4. As total lengths reached 150 to 165 μ the hinge-line was obscured by the appearance of a low, rounded umbo which subsequently developed into a knobby protrusion.

5. Pigmented eyespots began appearang as larvae exceeded 270 μ in size, and the full-grown foot of the pediveliger became functional as larvae surpassed 295 μ in length.

6. Discrimination of *Modiolus modiolus* and *Mytilus edulis* veligers is generally possible through a comparison of the following larval characteristics: hinge-line lengths, total shell length in the 95 to 105 μ range, shell shape of umbo stage larvae, presence of an eyespot in specimens with lengths less than 270 μ, and presence of a functional foot in larvae less than 295 μ.

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